

**Mechanisms Involved in the Pollination of  
*Penstemon* Visited by the Masarid Wasp,  
*Pseudomasaris vespoides* (Cresson)**

(Hymenoptera: Vespoidea)

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INTRODUCTION

*Pseudomasaris* is a North American representative of the vespoid wasp subfamily Masarinae. This subfamily, which is easily distinguished by clavate antennae, is unique among foraging wasps in that it provisions cells with pollen and nectar rather than with other arthropods. Bequaert (1940) and Cooper & Bequaert (1951) reviewed the flower records of masarids and listed the host plants visited by these wasps, but it was Cooper (1952) who first discussed the oligolectic habits expressed within *Pseudomasaris*. He concluded that these wasps collect pollen and nectar primarily from three hosts [*Phacelia*, *Eriodictyon* (Hydrophyllaceae) and *Penstemon* (Scrophulariaceae)] and suggested that wasp size was associated with the flower size found on host plant species. Therefore, the smallest species [*Pseudomasaris edwardsii* (Cresson)] visit *Phacelia* flowers, the largest species [*P. vespoides* (Cresson)] are restricted to *Penstemon*, and one intermediate-sized species [*P. wheeleri* Bequaert] visits both *Eriodictyon* and *Penstemon*. Cooper's tenets have since been confirmed by Straw (1956a, b), Richards (1962), Crosswhite & Crosswhite (1966), and Torchio (1970).

Pennell (1935) pointed to the fact that *Penstemon* is probably not surpassed by any other genus of flowering plants in the expression of different flower forms between species. Straw (1956b) described and figured the flowers of three species of *Penstemon* [section *Peltanthera* (Keck, 1937)] and discussed how the differences in form and color between them were associated with their pollinators. Thus, *P. centranthifolius* Bentham is pollinated by hummingbirds, *P. palmeri* Gray is pollinated by bumblebees (*Bombus* spp.) and carpenter bees (*Xylocopa* spp.), and *P. spectabilis* Thurber ex Gray is pollinated by *Pseudomasaris vespoides*.

Straw's discussion of wasp-pollinated *Penstemon* species was the

first attempt to describe the adaptive features involved in the pollinating mechanism of these flowers. He recognized the importance of pollinators fitting the form and size of flowers closely and learned that the lateral position of the nectaries in conjunction with the particular angulation of the flower serves to protect the ovary from damage by the probing proboscises of pollinators. He did not, however, discuss other important pollinating mechanisms of these flowers, and his interpretation of function for particular flower structures was incomplete.

The present paper describes the pollinating mechanisms found in *Penstemon* species visited by *Pseudomasaris* wasps.

#### METHODS

Numerous observations of pollen and nectar collections from *Penstemon* by *Pseudomasaris vespoidea* were made during biological studies in a greenhouse at Logan, Utah. Wasps were captured in the field and released in a greenhouse supplied with bouquets of *Penstemon sepalulus* A. Nels. and *P. cyananthus* Hook. and with potted plants of the latter. Fresh bouquets were supplied daily, and the wasps nested successfully. Dissections of these flowers in conjunction with additional field observations demonstrated that flower and wasp structures are synchronized to effect successful pollination.

#### ADAPTIVE FLORAL MECHANISMS

*Staminode*: *Penstemon* is distinctive from other Scrophulariaceae in its retention of the fifth stamen as a prominent, sterile filament. This filament, or staminode, arises on the inner-dorsal surface of the sympetalous corolla at various points (species dependent) along the basal third of the tube and bisects the throat of the flower at various angles until it turns and parallels the inner-ventral surface of the corolla tube where it ends at or near the mouth of the flower. The apical area of the staminode in some *Penstemon* species (*P. cyananthus*) is ornamented with shaggy hairs, whereas the staminode is devoid of hairs in other species (*P. sepalulus*). The outer-dorsal surface of the corolla tube directly above the insertion of the staminode is demarked by a linear depression in those *Penstemon* species studied (Fig. 1). This surface also possesses a narrow, keel-shaped ridge that arises immediately anterior of the depression and terminates near the apical tip of the tube (Fig. 1). The inner-dorsal surface of the corolla directly beneath the ridge is inverted into an elongate depression. The style is positioned dorsally so that the sub-basal section is adjacent to the

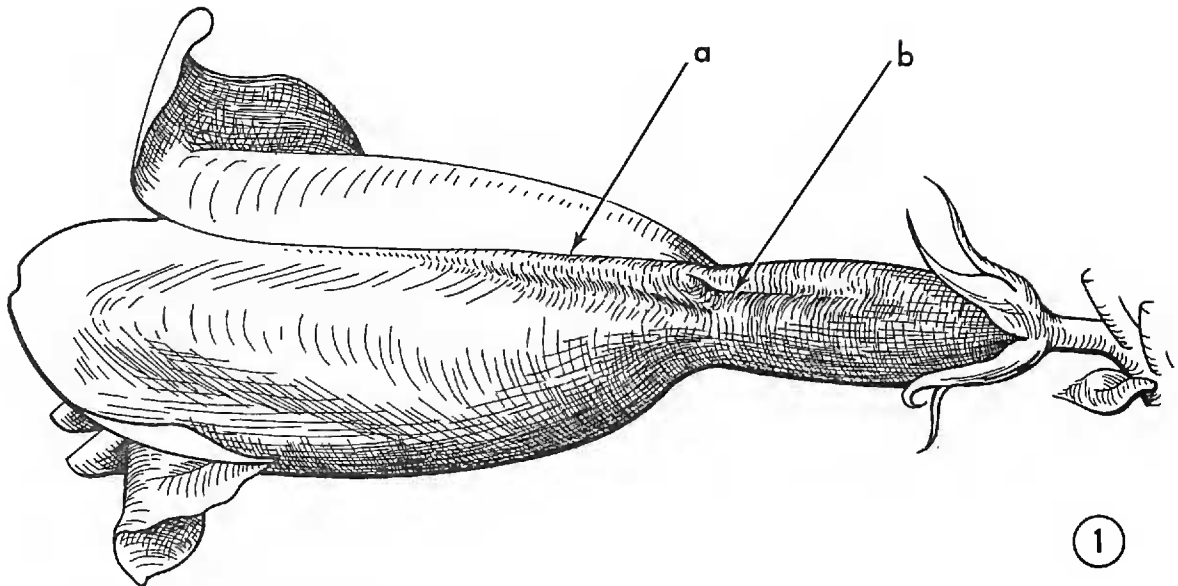


FIG. 1. Outer-dorsal view of *Penstemon cyananthus* flower showing: [a] ridge above style insertion; and, [b] corolla depression at staminode insertion.

staminode insertion, and its apical section is normally fitted into the linear depression of the inner-dorsal surface of the corolla tube.

Delpino (1875) presumed that the staminode serves to aid pollinators in locating nectaries; Kerner (1876) and Errera (1878) concluded that the dorsal to ventral position of this filament traversing the throat of flowers imposes a barrier that prevents or strongly reduces the incidence of nectar robbing by small insects with short tongues. Straw (1956b) discounted Delpino's theory, but he accepted the Kerner and Errera proposal.

The staminode in *Penstemon* flowers visited by *Pseudomasaris* wasps may actually function as a nectar guide (see discussion) and, at the same time, may serve as a mechanical barrier that reduces nectar robbing by smaller arthropods. Its main function, however, is to trigger pollination. This mechanism is initiated when the wasp enters the flower and pushes against the nearly vertical basal section of the staminode. When the wasp extends its proboscis to probe the flower for nectar, it habitually jerks its body back and forth as it rams the filament repeatedly with its head. If sufficient force is applied to the filament during any particular thrust by the wasp, the staminode is pushed inward (basad) a short distance, thus placing stress on the area of staminode insertion. This area functions as a fulcrum for the translocated pressure (due primarily to the angulation of the filament and the weaker corolla structure surrounding the depressed insertion area). Thus, outward pressure is applied to the basal section of the staminode insertion, and an equal but opposite pull-force develops

across the anterior section. Invariably, the pull-pressure is sufficiently great to bend a short transverse section of the corolla tube anterior of the insertion area downward as the staminode is pushed slightly backwards. Since the sub-basal section of the style is always found appressed against the inner-dorsal surface of the corolla tube adjacent to the staminode insertion, it too is pushed downward when the small section of corolla tube in front of the staminode insertion is forcibly indented. If the stigma is receptive (anterior section of style bent downward), the downward movement of the style causes the stigma to touch the pollen-laden scutum of the wasp. The style springs back to its original position when pressure is removed from the staminode, but it will move downward each time the wasp rams the staminode. This adaptive mechanism not only assures pollination, but it also facilitates a higher probability for cross pollination.

*Stamens*: Protandry as a mechanism to better facilitate outcrossing is well known in *Penstemon*. Clements and Long (1923, plate 12) illustrated the typical maturation process of these flowers, and Straw (1956b) discussed the sequential development of flower structures during anthesis. In those species studied, in Utah, the anterior pair of anthers mature shortly after the flower opens, but dehiscence by the shorter pair (upper) is delayed 12–15 hours. The stigma begins to turn downward to its receptive position 6–12 hours after the shorter pair of anthers begins to dehisce, which decreases the probability of selfing.

Most of the pollen grains in *Penstemon* flowers visited by *Pseudomasaris* wasps are retained in the anthers after dehiscence, and only a few are released each time the dehisced anthers are vibrated. Pollen dispersion, therefore, occurs after the wasp enters the flower and positions its scutum and scutellum to face the elongate openings of the dehisced anthers. Each opening is guarded by a row of short, stiff, strong spines that rub across the thoracic surface of the wasp when the insect begins to move backward and forward during its nectar collecting activities. The scraping of thecal spines across the rough surface of the insect's thorax (sometimes heard as a clicking sound in flowers of *P. cyananthus*) initiates vibration of the anthers, which results in the release of pollen grains directly onto the wasp's scutellum. Therefore, this mechanism has varied functions: (1) it releases pollen onto appropriate pollinators; (2) it deposits pollen directly on that surface of the insect which is subsequently touched by the stigma; (3) it permits pollen from each theca to be deposited on a number of wasps over an extended period to better facilitate outcrossing (the delayed

dehiscence of the shorter anther pair also increases the period of pollen release); and, (4) it serves to prevent or impair pollen robbing by other *Penstemon*-visiting insects because of the position of the anthers, the long narrow dehiscence line of each theca, and the guard spines.

Obviously the pollinators of *Penstemon* also possess adaptive features that insure successful pollination. Straw (1956b) discussed such apparent points as body size and form. However, two additional features should be mentioned in the case of *Pseudomasaris*. One is the elongate, nearly flat-surfaced scutum that is covered laterally with sparse, erect hairs. This structure should be considered adaptive because its extreme length accommodates at least the anterior anthers, irrespective of variation in the size of individual flowers or wasps; and the erect hairs function to accept and hold pollen grains in place, which prevents pollen dispersion over a large surface area. The scutellum is also elongated and could be considered a posterior extension of the thoracic surface that receives *Penstemon* pollen. The transfer of pollen from the wasp's mesonotum to the proboscis with specific preening movements of the front legs should also be considered adaptive. This combing activity with specialized hairs transfers most of the pollen, but it also mixes a residue of the pollen grains collected from different flowers across the surface of the thorax, thus increasing the probability of outcrossing.

*Style*: Clements and Long (1923, plate 12) illustrated how the style of *Penstemon glaber* Pursh elongates as the open flower matures, but this structure is fully extended as flowers open in *P. cyananthus* and *P. sepalulus*. The length of the style in these two species is also variable. Thus, the stigma on the shortest style is located slightly distad of the upper (shorter) stamens, and the longest style has the stigma positioned between or slightly distad of the longer stamens. Further, variation in style length occurs on the same or different racemes of the same plant in either species. These variations, coupled with variation in the size of flowers and wasps, increase the effective surface area of the wasp's thorax that is utilized for pollen transfer to the stigma; and at the same time, they increase the probability of cross pollination.

The primary mechanism that forces the style to move downward (infolding of corolla tube distad of staminode insertion) has already been described, but additional flower structures should be included as supportive mechanisms of this movement. The groove on the inner-dorsal surface of the corolla tube in which the style is inserted is one such structure. Its presence prevents the style from swinging back and forth laterally whenever the flower is moved, thus reducing the chance

of its entanglement with the anthers or staminal filaments. If entanglement occurs, the style can no longer move vertically; and its normal function is lost.

Lateral migration of stamens also occurs before the style fully matures. When the flower first opens, the stamens are positioned with their anthers nearly touching each other. By the time dehiscence is initiated, the anthers have migrated a short distance away from each other and the resulting space is sufficiently wide to permit the style to pass between them.

Straw (1956b) discussed how the position of the ovary below the midline of the corolla and the position of the nectaries at the outer bases of the upper stamens served to protect the ovule against mechanical damage when pollinators probe flowers for nectar. The direction and position of both pairs of stamens may serve the same function. The shorter pair arises laterad of the ovary and converges in front of it. These stamens then diverge as they appress against the upper wall of the corolla tube. The longer stamens arise below the ovary and nearly parallel the shorter stamens as they converge in front of the ovary. Together, the four stamens almost completely surround the ovary, thus protecting it against mechanical damage by pollinators and other arthropods.

#### DISCUSSION

The foregoing descriptions suggest that those species of *Penstemon* visited by *Pseudomasaris* wasps have evolved particular floral mechanisms that are well adapted to these oligolectic pollinators. In addition, Straw (1956b) discussed various floral mechanisms found in many *Penstemon* species that are particularly well adapted to other pollinators including hummingbirds and bees. Yet, the position and form of most flower structures in this taxon are sufficiently similar to indicate that particular functions are retained at the generic level irrespective of most adaptive mechanisms associated with oligolectic or monolectic pollinators. The staminode, for example, has the primary function of triggering pollination in those *Penstemon* species visited by *Pseudomasaris* wasps. Conversely, the staminode does not possess this function in *Penstemon* flowers pollinated by hummingbirds, bombyliid flies, and some bees; though the filament is retained as a prominent floral structure in the genus. Therefore, the staminode is a multifunctional structure that has evolved in some species as an adaptive mechanism to trigger or facilitate pollination, and at the same time, performs other functions that are expressed in all *Penstemon* flowers. To date, no direct evidence has been presented to explain what these

functions are, but Delpino (1875) suggested that the sterile filament serves as a nectar guide, and Kerner (1876) and Errera (1878) proposed that it acts as a barrier to small, nectar-robbing arthropods.

Observations during the present study tend to support Delpino's contention that the staminode does indeed act as a nectar guide. Also, the filaments of the upper stamens, in conjunction with the staminode, serve as nectar guides once the wasp enters the flower and touches its head against the staminode. The midline of the wasp's head appresses against the filament, which is automatically positioned directly in front of the pollinator's mouthparts. When the wasp begins to extend its proboscis into the throat of the flower, the tongue hits the staminode, which in turn causes it to be deflected to one side or the other in the general direction of the laterally positioned nectaries. When the tongue is further extended, it normally touches one of the two filaments of the upper stamens each of which is angulated in such a way as to further guide the tongue toward a nectary. Additionally, observations indicated that the staminode does act as a barrier to some bee visitors (two species of *Osmia* and one species of *Andrena*), but not to others (one species of *Hylaeus*, one species of *Osmia*, and one species of *Halictus*). Apparently, the workability of the barrier is dependent upon two factors: (1) the size of each opening in the corolla tube that is present on either side of the staminode, and (2) the angulation of that staminode in relation to the particular form of each *Penstemon* flower. If the opening of the corolla tube on either side of the staminode is larger than the diameter of the arthropod visitor, that insect can crawl directly to the nectaries and rob them. Conversely, if either opening is smaller than the diameter of the visitor's body, the staminode bars its entrance.

Angulation of the staminode is sometimes important because it prevents "robbing" by non-adaptive pollinators whose tongues are sufficiently long to reach the nectaries should their heads touch the staminode insertion (some *Osmia*, *Hoplitis*, etc.). However, the heads of these long-tongued bees are usually more elongate and/or broader than those of *Pseudomasaris* and require a larger corolla tube opening in front of the staminode insertion. The size of this space is limited dorsally by the corolla tube and ventrally by the staminode filament. Therefore, the particular angulation of the filament determines the vertical diameter of this space (the greater the angulation of the staminode, the greater the vertical diameter of the space). Invariably this opening proves too narrow to accommodate full entrance by long-tongued, non-adaptive bee visitors, and robbing is thus thwarted.

Information presented here is derived from the study of only two wasp-pollinated species of *Penstemon* in a limited geographical area. The genus, however, is a relatively large, North American taxon that is associated with many specific pollinators. Consequently, additional pollination studies must be completed before all the adaptive floral mechanisms expressed in the taxon can be understood. With a definitive understanding of these pollination mechanisms in *Penstemon* (a popular introduced plant in other parts of the world), we should be better able to determine which species groups can be successfully established in areas outside their normal ranges.

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### BOOK NOTICE

BIOLOGICAL CONTROL BY NATURAL ENEMIES. Paul Debach. Cambridge University Press, London and New York. 323 pp. 1974. Cloth, \$14.95; paper, \$5.95.

This semi-technical book should attract a wide audience among non-entomologists and entomologists alike. Written in a clear, informative style, and appended by a functional but not overwhelming bibliography, it provides a useful overview of the field, while allowing enjoyable reading at the same time. The first and last chapters discuss pesticide usage and problems. Relatively short sections describe the biological characteristics of natural enemies of pests (insects and weeds), applied ecology, the role of science and the public, and a survey of cultural, genetic, and other non-chemical methods of control. About one third of the book relates case histories of the more important biological control projects. Especially fascinating are the accounts of early foreign exploration. The dedication and endurance of many of the pioneering workers, who usually labored under extremely primitive conditions, recall the earlier biological expeditions of the 18th and 19th centuries. Perhaps the fervor of these hardy individuals set a historical precedent which partly explains the zeal of many contemporary practitioners of biological control.—EDITOR.